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Semantic and attentional networks in bilingual processing: fMRI connectivity signatures of translation directionality

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Abstract

Comparisons between backward and forward translation (BT, FT) have long illuminated the organization of bilingual memory, with neuroscientific evidence indicating that FT would involve greater linguistic and attentional demands. However, no study has directly assessed the *functional interaction* between relevant mechanisms. Against this background, we conducted the first fMRI investigation of functional connectivity (FC) differences between BT and FT. In addition to yielding lower behavioral outcomes, FT was characterized by increased FC between a core semantic hub (the left anterior temporal lobe, ATL) and key nodes of attentional and vigilance networks (left inferior frontal, left orbitofrontal, and bilateral parietal clusters). Instead, distinct FC patterns for BT emerged only between the left ATL and the right thalamus, a region implicated in automatic relaying of sensory information to cortical regions. Therefore, FT seems to involve enhanced coupling between semantic and attentional mechanisms, suggesting that asymmetries in cross-language processing reflect dynamic interactions between linguistic and domain-general systems.

Keywords: bilingualism, translation, fMRI, functional connectivity, semantic networks, attentional networks.

1. Introduction

One of the distinguishing traits of bilingual memory is the capacity to engage in backward and forward translation –BT and FT, respectively (de Groot et al., 1994; Duyck & Brysbaert, 2004, 2008; van Hell & de Groot, 1998; Kroll & Stewart, 1994; Kroll et al., 2010). These two operations involve crosslinguistic processes between a bilingual’s first and second languages (L1 and L2). In BT, the L2 functions as source language and the L1 serves as target language, whereas FT involves cross-linguistic processes from L1 (source language) to L2 (target language) (Pokorn, 2011). Neuroscientific assessments of this contrast (Christoffels et al., 2013; Jost et al., 2018; Klein et al., 1995; Quaresima et al., 2002; Rinne et al., 2000; Tommola et al., 2001) have illuminated the task-dependent interplay between linguistic and attentional processes in different bilingual populations, offering hints on the role of domain-general mechanisms during cross-linguistic production. However, such experiments have focused exclusively on regional activity changes (García, 2013), overlooking *functional interactions* among segregated neurocognitive hubs. This is a major shortcoming in the literature, given that cognitive operations are increasingly recognized as dependent on the co-activation of distributed brain areas (Mišić & Sporns, 2016). To bridge this gap, we conducted the first assessment of functional connectivity (FC) differences between BT and FT.

Both BT and FT involve three macro-phases, each recruiting interactive linguistic mechanisms mediated by cognitive control operations. As recognized by different models in translation studies and bilingualism research (Bell, 1991; Gile, 1991; Paradis, 1994; Ruiz et al., 2007; Seleskovitch, 1978), these phases consist in source-text processing (which encompasses operations like letter recognition and integration, lexical access, morphosyntactic parsing, and semantic activation), interlinguistic processing (which consists in the establishment of cross-language associations via form-level and conceptually mediated

links), and target-text processing (through operations like lexical selection, morphosyntactic integration, and phonological or graphemic production). However, each direction differs in the demands it places on these mechanisms. In particular, although source-text processing effort is typically higher for BT than FT –arguably due to greater lexico-semantic demands associated with processing input in L2 as opposed to L1 (e.g., Christoffels et al., 2013), *overall* behavioral performance is typically worse for FT than BT (e.g., Darò et al., 1996; de Groot et al., 1994; Hatzidaki & Pothos, 2008; Jost et al., 2018; Kroll & Stewart, 1990; Kroll & Stewart, 1994; Sánchez-Casas et al., 1992).

Foundational psycholinguistic explanations (French & Jacquet, 2004) and recent computational models (Dijkstra et al., 2018) of this phenomenon have emphasized lexico-semantic factors, claiming that it reflects asymmetrical strengths in form-level and conceptually-mediated connections between L1 and L2 systems. The most explicit account in this sense has been offered by the revised hierarchical model (RHM; Kroll & Stewart, 1994; Kroll et al., 2010). Drawing on evidence from word translation tasks and other relevant paradigms, this model posits that cross-linguistic processing during FT would be more critically afforded by concept-level connections, whereas BT would more critically depend on form-level connections –although these differences are typically attenuated at high levels of L2 proficiency or translation competence (García et al., 2014; Kroll & Stewart, 1994; Santilli et al., 2018; for a review, see García, 2015). Seen from this vantage point, directionality effects would be mainly driven by the configuration of lexico-semantic systems in bilingual memory (French & Jacquet, 2004).

However, other classic models (Green, 1998) nurture a more complex view, indicating that differences between BT and FT cannot be solely explained in terms of linguistic factors. In this sense, the inhibitory control model (Green, 1998) posits that verbal processing in bilinguals requires selecting and coordinating language task schemas into functional control circuits that, in turn, modulate the mental representations of word meanings and word forms. In this sense, FT would be characterized by greater monitoring and regulating effort from the supervisory attentional system (Green, 1998). This would be so because connections between source-language forms and meanings are typically weaker for BT than FT (so that within-language competition is more readily suppressed in the former) and target-language items can be more readily activated in L1 than L2. From this perspective, then, directionality effects would result from a combination of linguistic *and* cognitive control factors.

Neuroscientific evidence aligns with the latter position, showing that differential activations between BT and FT, and lesions resulting in selective deficits for one of these tasks, can be traced to regions subserving verbal and non-verbal domains (García, 2013). Broadly speaking, processing of translation equivalents hinges on widely distributed areas. In particular, anterior temporal regions subserving verbal and non-verbal semantic operations play a key role in processing conceptual information shared between translation equivalents (Correia et al., 2014). Also, inferior frontal areas implicated in morphosyntactic processing (Grodzinsky & Friederici, 2006; Ullman, 2001b; Zaccarella & Friederici, 2016) are significantly engaged during sentence translation (Lehtonen et al., 2005; Rinne et al., 2000). In addition, evidence of increased activity along parietal and prefrontal/orbitofrontal sites during translation has been proposed to reflect the recruitment of attentional, inhibitory, and working memory mechanisms (Jost et al., 2018; Klein et al., 1995), suggesting a general involvement of cognitive control mechanisms (Abutalebi & Green, 2007; Luk et al., 2011; Miyake & Friedman, 2012; Miyake et al., 2000). Still, each direction involves different neurocognitive demands.

On the one hand, evidence of increased modulations for BT relative to FT is scant, with one neuroscientific study (Christoffels et al., 2013) suggesting more effortful semantic access to (L2) input words and other reports failing to detect any significant pattern across

methods and techniques (Jost et al., 2018; Klein et al., 1995; Quaresima et al., 2002; Rinne et al., 2000; Tammola et al., 2001). Yet, on the other hand, FT seems consistently characterized by greater activation than BT in perisylvian and frontostriatal sites (Quaresima et al., 2002; Rinne et al., 2000; Tammola et al., 2001), many of which subserve linguistic processes (Birba et al., 2017; Pulvermüller, 2018) and constitute key hubs of the frontoparietal network – implicated in cognitive control (Zhang et al., 2015)– and the vigilance network –which mediates attention allocation over brief cognitive events (Shen et al., 2016). Indeed, relative to BT, FT involves stronger electrophysiological modulations traceable to areas mediating vigilance and arousal (Jost et al., 2018) and greater amplitude of the P2 component, a sensitive index of attentional demands (Christoffels et al., 2013). Therefore, the distinctive effects typifying FT seem driven by both semantic *and* attentional processes.

Nevertheless, the *dynamic coupling* of such mechanisms during translation remains poorly understood, as the interaction of distributed neuronal populations cannot be directly examined through the purely regional and univariate approximations used so far in the field (Mišić & Sporns, 2016). Promisingly, relevant insights can be obtained via FC metrics, which rely on statistical dependencies between remote regions to reveal whether they are *exchanging* information during a particular process (Buzsáki, 2006; Friston, 2011; Velazquez & Wennberg, 2009; Varela et al., 2001), even when no significant effects are manifested in regional activation changes (Mišić & Sporns, 2016). In this sense, the only FC study on directionality, based on scalp-level and intracranial electroencephalography (García et al., 2016), offered preliminary evidence that FT of single words involved greater fronto-temporo-parietal coupling than BT, suggesting greater executive and semantic demands. However, given the low spatial resolution of scalp-level EEG and the limited anatomical coverage of intracranial EEG, such results prove inconclusive and invite more spatially precise approximations.

This scenario gives rise to a relevant research question: which FC patterns, if any, underlie the increased cognitive control demands typifying linguistic operations in FT? To address this question, we conducted the first fMRI assessment of FC differences between BT and FT, relative to their respective baseline reading conditions. Considering the findings above, we hypothesized that FT would involve greater FC along fronto-temporo-parietal networks mediating both linguistic and attentional processes. To test this conjecture, we asked high-proficiency bilinguals to overtly translate and repeat naturalistic sentences in their L1 (Mandarin Chinese) and L2 (English) as we obtained event-related fMRI recordings to assess FC changes via psychophysical interaction (PPI) analyses (Friston, 2011; O'Reilly et al., 2012). Specifically, to examine whether language-sensitive areas interacted differentially with attentional hubs during each task, we used a seed analysis targeting regions of interest (ROIs) associated with semantic and morphosyntactic processing within and across languages: the left anterior temporal lobe (ATL) (Correia et al., 2014; Lambon Ralph et al., 2017; Patterson et al., 2007) and the left inferior frontal gyrus (IFG) (Grodzinsky & Friederici, 2006; Lehtonen et al., 2005; Rinne et al., 2000; Ullman, 2001b; Zaccarella & Friederici, 2016). In addition, to gain further insights on the potential specificity of ATL-related effects we replicated our analysis over another ROI associated with semantic processing in verbal tasks, namely, the left posterior middle temporal gyrus (pMTG) (Noonan et al., 2013). Finally, to directly test whether FC analyses can capture effects that escape typical univariate approximations, we mirrored all key comparisons via regional activation analyses. In short, with this approach, we aimed to shed light on the synergies between linguistic and domain-general mechanisms during bilingual processing.

2. Methods

2.1. Participants

Upon exclusion of two participants due to excessive motion artefacts, the final sample comprised 25 female Mandarin-Chinese speakers (mean age = 23.92, $SD = 0.91$) who learned English at an average age of 9.36 ($SD = 0.49$). All subjects were MA translation students from UK universities with an average of 1.8 ($SD = 0.87$) years of training in translation and interpreting. Results from the IELTS test indicated that, in a range of 1 ('non-user') through 9 ('expert user'), the sample had a mean score of 7.44 ($SD = 0.39$), corresponding to 'very good users' with full command of the language, elevated argumentative skills, and only sporadic inaccuracies and difficulties (for details about the test's nine-band scale, see Supplementary materials, section 1). They all had normal or corrected-to-normal vision and they were confirmed as right-handers through the Edinburgh Handedness Inventory (Oldfield, 1971). No participant had a history of neurological or psychiatric disorders or alcohol abuse. All subjects were paid for their participation and provided written informed consent. The experiment was conducted in accordance with the Declaration of Helsinki and approved by ethics committee of Durham University.

2.2. Materials

The stimulus set contained 96 sentences, half in English and half in Mandarin Chinese (see Supplementary materials, section 2). The English stimuli were extracted and adapted from the subtitles of *Fantastic Mr Fox*, which can be freely accessed on the IMSDb website (<https://www.imsdb.com/scripts/Fantastic-Mr-Fox.html>) and subjected to fair use without infringement of copyright. The Mandarin Chinese stimuli (created by the authors specifically for the present study, under no copyright) possessed similar syntactic structures but different meanings relative to the English stimuli). All sentences were simple, declarative, affirmative, non-marked, and idiomatic, with no complex noun phrases. Strategically, sentences featuring a colloquial register were kept unaltered to guarantee their ecological validity and thus render the study more informative about real-life scenarios during translation. Ratings from ten proficient Chinese-English bilinguals showed that both sentence sets were not statistically different in terms of grammaticality [$t(94) = -1.60, p = .11$], coherence [$t(94) = -1.68, p = .10$], comprehensibility [$t(94) = 1.64, p = .10$], and translatability [$t(94) = 1.47, p = .14$]. The two sets were also similar in their mean number of content words [$t(94) = -0.92, p = .36$] and identical in their distribution of personal pronouns. Moreover, data from the SUBTLEX-UK (van Heuven et al., 2014) and SUBTLEX-CH (Cai & Brysbaert, 2010) databases showed that mean content-word frequency did not differ between the two sets [$t(379) = -0.52, p = .61$]. Finally, note that, with the exception of two words (*Kitty*, 凯蒂 [Kai di]; *golf*, 高尔夫 [Gao er fu]), all lexical items were classified as noncognates based on criteria by (Wen & van Heuven, 2017).

2.3. Task design

The experiment included four conditions (L1R, L2R, BT, FT), counterbalanced across participants. Each condition comprised 24 sentences, presented in blocks of four pseudo-randomly chosen trials. Each block started with a task-instruction slide lasting 18 seconds, which prevented confounds triggered by the alternation of tasks and languages. The sentences were arranged in two left-aligned lines, presented against a black background in white fonts

(English: Arial, size 40; Chinese: SimHei, size 40). Trials in the reading and translation conditions were shown for 8 and 15 seconds, respectively (Figure 1). All stimuli were constructed and delivered via E-prime 2.0.

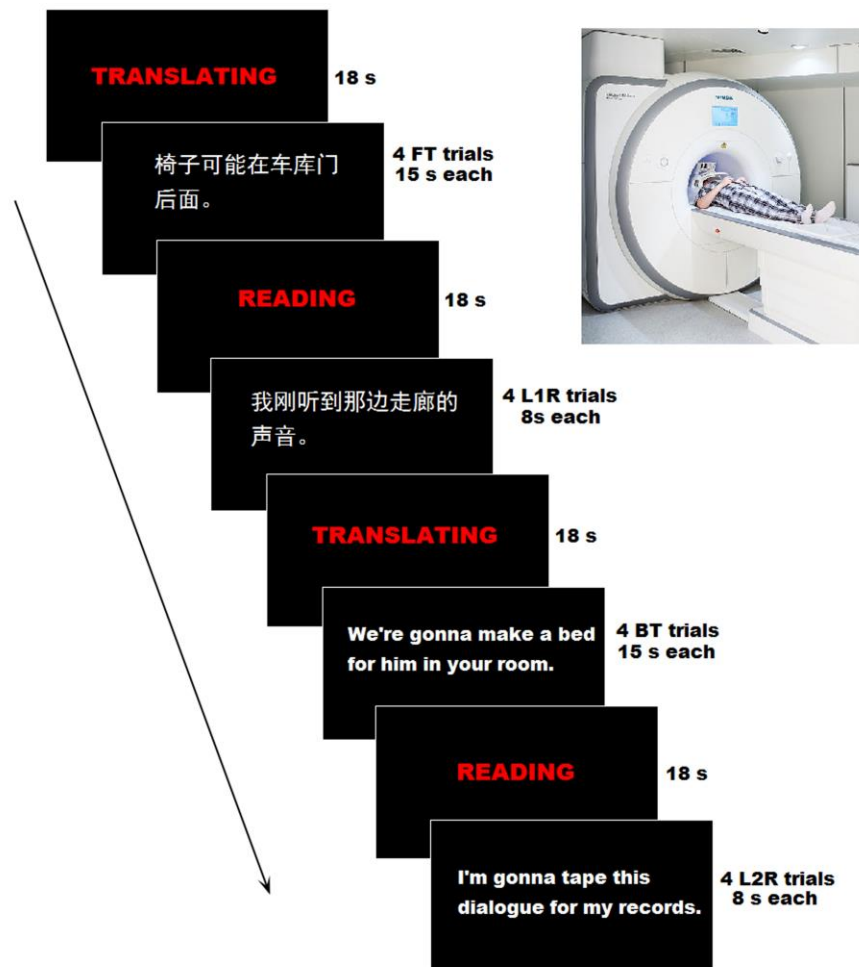


Figure 1. Task design. The experiment included four conditions: first-language reading (L1R), second-language reading (L2R), backward translation (BT), and forward translation (FT). Each condition comprised 24 sentences, presented in blocks of four pseudo-randomly chosen trials. Each block started with a task-instruction slide lasting 18 seconds. Trials in the reading and translation conditions were shown for 8 and 15 seconds, respectively. MRI scanner figure by Peggy.poon.ths [CC BY-SA 4.0 (<https://creativecommons.org/licenses/by-sa/4.0>)], from Wikimedia Commons.

2.4. Procedure

Scanning sessions were conducted individually at Durham University's MRI Facility. Participants were first informed about the experiment and asked to complete a questionnaire tapping on demographic and language history information. Once inside the scanner, they were asked to complete four practice trials from each task. During scanning, each participant was instructed to either read out loud (L1R, L2R) or sight translate (BT, FT) the trials appearing on the screen, as fast and accurately as possible. Their verbal responses were recorded with BOLDfonic's MRI-compatible audio solution for offline assessment. Each session lasted roughly 30 minutes.

2.5. Imaging methods

2.5.1. MRI data acquisition

MRI acquisition and preprocessing steps are reported following gold-standard guidelines (Nichols et al., 2017). Data were collected with a Siemens 3-T Trio MRI scanner, fitted with a 32-channel head-coil. A high-resolution T1-weighted image was acquired for each subject (TR = 2250 ms, TE = 2.52 ms, field of view (FOV) = 256×256 mm, matrix = 256×256 , 192 slices, spatial resolution = $1 \times 1 \times 1$ mm³). Functional images were obtained from 35 gradient-echo T2*-weighted slices per volume (TR = 2160 ms, TE = 30 ms, flip angle of 90°, FOV = 210×210 mm, matrix = 96×96).

2.5.2. fMRI data preprocessing

Functional images were analyzed using SPM8 (www.fil.ion.ucl.ac.uk/spm/software/spm8). In line with validated procedures (Kanske et al., 2016; Kanske et al., 2015), images were realigned and the subject's mean was co-registered with the corresponding structural MRI. These images were subsequently slice-time corrected, spatially normalized, and transformed into a common space, as defined by the MNI space. The normalized images were spatially smoothed with a Gaussian kernel of full-width half-maximum at 8 mm.

Given that the ATL may be subject to distortion and signal dropout in fMRI (Devlin et al., 2000), potentially precluding the detection of relevant activation patterns, we established our data quality by calculating its temporal signal-to-noise ratio (TSNR). Following previous procedures (Philip & Frey, 2016; Sander et al., 2007; Simmons et al., 2010), TSNR was calculated by dividing the mean signal intensity at a voxel level by the standard deviation of its signal's time course.

2.5.3. Regional activation analysis

After preprocessing, statistical analyses were performed on individual participant data using general linear models (GLMs). Effects of interest were convolved with a canonical hemodynamic response function. To make comparable reading and translation conditions, we analyzed the BOLD signal within the first 2 seconds after sentence onset. Previous fMRI studies on translation reporting signal acquisition over spans of 2.1 seconds (Hervais-Adelman et al., 2015a), together with previous neuroimaging studies on sentence translation presenting stimuli every 3 seconds (Quaresima et al., 2002) and evidence that fluent English-Mandarin bilinguals take around 1.5 seconds to read and understand sentences in both languages (Chee et al., 1999), suggest that this time window is appropriate to analyze the BOLD signal and track FC differences between BT and FT. One regressor for each condition was specified. Additionally, six subject-specific movement regressors were included as covariates of no interest. Serial correlations in the time series were accounted for using the autoregressive model. A temporal high pass filter of 128 s was used.

Following previous procedures (Rosenberg-Katz et al., 2016; Van Overwalle & Marien, 2016), we implemented multiple steps to control for potential motion artifacts. First, the motion parameters for translation (i.e., x , y , and z) and rotation (i.e., yaw, pitch, and roll) were included as covariates of non-interest in the GLM. Therefore, potential FC differences

between conditions could not be attributed to distinct motion-related patterns in each of them. In addition, to further reduce the influence of potential noise-related biases, data were examined for excessive motion artifacts and for correlations between motion or global mean signal and any of the conditions using the Artifact Detection Tool (ART) software package (www.nitrc.org/projects/artifact_detect). Subjects with outlier motion-parameter values were identified in the temporal difference series by assessing between-scan differences (global mean intensity 3 SDs from the entire time series, scan-to-scan movement threshold: 3 mm; rotation threshold: 0.02 radians). As stated in the “Participants” section, this resulted in the exclusion of two subjects, leading to the final sample of 25 individuals. No correlations between motion or global signal and experimental conditions were identified.

Contrast images (for L1R vs. L2R, FT vs. BT) were then calculated by applying linear weights to the parameter estimates and entered into one-sample *t*-tests for random effects analysis. A two-sample *t*-test was also performed to compare FT and BT relative to their respective baseline reading-task conditions [(FT > L1R) vs. (BT > L2R)]. Following standard recommendations (Poldrack et al., 2017) and previous fMRI reports (e.g., Macedonia et al., 2019; Seubert et al., 2010; Uluc et al., 2018), the activation reported was under the threshold of $p < .05$, family-wise-error-(FWE)-corrected, with a minimum cluster size of 30 contiguous voxels. For all group-level analyses, the participants’ behavioral outcomes were included as covariates of interest. Specifically, for the L1R vs. L2R and the FT vs. BT contrasts, analyses were covaried with the mean accuracy for reading or translation tasks, respectively. Finally, for the double contrast [(FT > L1R) vs. (BT > L2R)], we included two covariates: FT accuracy minus L1R accuracy, and BT accuracy minus L2R accuracy.

2.5.4. ROI selection criteria

Our analysis focused on three language-sensitive ROIs, namely: the left ATL, the left IFG, and the left pMTG. These regions play putative roles in key functions implicated by our task—crucially including semantic (Lambon Ralph et al., 2017) and morphosyntactic (Ullman, 2001b; Zaccarella & Friederici, 2016) processing—and they have been shown to be critically involved in cross-linguistic mappings (Correia et al., 2014; Klein et al., 1995; Rinne et al., 2000; Tammola et al., 2001). In particular, by focusing on language-sensitive ROIs, as opposed to others distinctively implicated in attentional/control functions, we prevented the possibility of false negatives between our conditions. This is so because, for high-proficiency bilinguals, between-language differences in attentional/control hubs may prove too subtle (Chee et al., 1999; Videsott et al., 2010) to be captured by the PPI method. Also, given that attentional/control networks are widely distributed across the brain (Corbetta & Shulman, 2002; Hopfinger et al., 2000; Pessoa et al., 2003), choosing only a restricted number of attentional/control ROIs might have biased our results towards one specific condition—indeed, it is not yet clear how crucially each translation direction relies on particular hubs within such vast networks.

Therefore, the selection of ROIs related to semantic and morphosyntactic functions allowed us to examine FC patterns between linguistic and attentional/control hubs in each direction without the potential biases of selecting attentional ROIs differentially engaged by each translation direction. Considering our experimental design and aims, we established ROIs based on previous literature, as typically done in several studies using PPI analyses (Schott et al., 2019; Spotorno et al., 2012; Steffens et al., 2016). Importantly, although previous PPI studies on language (e.g., Oliver et al., 2017) have selected ROIs based on group or individual activation peaks relative to a task-unrelated baseline, our experiment did not lend itself to this approach because of three reasons. First, our design involved two language-specific

reading tasks as control conditions for each of the translation directions –as opposed to a common baseline for both conditions. Second, we aimed to assess *bidirectional* FC differences between BT and FT, relative to their respective baseline reading conditions. Therefore, selecting activation peaks for any one contrast (e.g., BT over FT, or BT over L2R) could bias results against the opposite contrast (e.g., FT over BT, or FT over L1R). Also, although individual activation peaks could be established based on aggregated data encompassing the different conditions, this procedure may underestimate the specific modulations for each translation condition. All of these shortcomings can be effectively circumvented through the use of previously reported ROIs, hence our decision to adopt this strategy.

In particular, following previous reports (Gilmore et al., 2018) we created our target ROIs by taking a sphere with a 10-mm radius around previously reported MNI coordinates. Specifically, for the left IFG we took coordinates (pars triangularis: -46, 28, 12) previously associated with tasks that directly or indirectly tax morphosyntactic processes (Liakakis et al., 2011). For the left ATL the ROI was centered on coordinates previously related to semantic processes (anterior middle temporal gyrus: -50, 3, -20) (Wilson et al., 2014). For the left pMTG, the ROI was centered on previous coordinates (posterior middle temporal gyrus: -54, -49, -1) also associated with semantic processing (Noonan et al., 2013).

2.5.5. Functional connectivity analysis

Functional interactions between our target ROIs and the rest of the brain were examined via PPI analysis, a robust method for investigating task-specific FC changes in fMRI research (Friston, 2011; O'Reilly et al., 2012), including neurolinguistic experiments (Kepinska et al., 2018). PPI analyses were conducted for every ROI separately on SPM-8. We first computed statistical contrasts between conditions using a GLM, including one regressor for each condition. The six movement artifact regressors were included as covariates of no interest. We employed a default high-pass filter of 128 s. Following previous evidence on bilingual translation (see details on regional activation analysis section), we analyzed the BOLD signal within the first 2 seconds after sentence onset.

PPI analysis was based on a linear model with three predictors. For each ROI, the deconvolved time series was extracted for each participant as the first regressor in the PPI analysis (physiological variable). The second regressor represented the experimental conditions (psychological variable): (a) L1R-L2R and (b) FT-BT. The third regressor was the interaction between the time series of the seed region and the experimental condition (PPI). To construct the PPI term, the deconvolved time-course of the seed regions was multiplied with a vector containing the psychological variables of interest. This product was then re-convolved with a canonical hemodynamic response function (Gitelman et al., 2003). The coefficient of this third (interaction term) is the one of interest in PPI analyses.

At the second-level analysis, for each ROI we computed one-sample *t*-tests to compare functional networks between experimental conditions: (a) L1R-L2R and (b) FT-BT. A two-sample *t*-test was also performed to compare FC between FT and BT, relative to their respective reading task baseline conditions [(FT > L1R) vs. (BT > L2R)]. Importantly, note that, in line with previous research (Price et al., 1999; Rinne et al., 2000; Tammola et al., 2001), direct contrasts between FT-minus-L1R and BT-minus-L2R allow comparing both translation directions while partly ruling out potential differences in the initial source-language processes they entail –for insights on these, see Chee (2009), Klein et al. (2006), Lucas et al. (2004), Ojemann & Whitaker (1978), Paradis (2009), Ullman (2001a), and Videsott et al. (2010).

Given that the expected effect size for PPI analyses would be much smaller than for a regional activation analysis of the main effect of a task (O'Reilly et al., 2012), we used a more lenient threshold with an uncorrected $p < .001$ and minimal cluster size $k = 30$. The avoidance of multiple comparisons correction was strategic because the statistical power of PPI analyses tends to involve a high proportion of false negatives (O'Reilly et al., 2012). Conversely, the selected thresholding procedure balances the risk of type I and type II errors (Lieberman & Cunningham, 2009), and it has been successfully employed in previous studies using PPI analyses (Baeuchl et al., 2015; Li et al., 2018; Osumi et al., 2012; Steuwe et al., 2015) as well as other FC metrics (Geisler et al., 2017; Lee et al., 2014; Loitfelder et al., 2012; Yasuno et al., 2015). For all group-level analyses, the subjects' behavioral outcomes were included as covariates of interest (see section 2.5.3 for details).

3. Results

3.1. Behavioral results

In line with reported criteria (Hervais-Adelman et al., 2015a; Hervais-Adelman et al., 2015b), verbal responses were assessed independently by two professional, accredited English-Chinese interpreters. Correct reading trials were allotted 1 point and incorrect ones were given 0 points. Translation responses were evaluated on a five-point scale: 0 = no output, 1 = only one correct content word, 2 = only two correct content words (minimally, a subject and object), 3 = meaningful overall translation with minor defects, 4 = flawless translation. Inter-rater reliability reached 99.58% for the reading assessment and 96.08% for the translation assessment. Mean accuracy was not significantly different between L1 reading (L1R) and L2 reading (L2R) [$t(24) = 0.92, p = .36$], but it proved significantly lower for FT than BT [$t(24) = 2.19, p = .04$]. Importantly, none of the participants expressed any surprise or difficulty concerning the register of the stimuli. Also, in the vast majority of cases, the translations they produced successfully captured these stylistic nuances –and, in the few instances in which this was not achieved, the response was scored as a “meaningful overall translation with minor defects.”

3.2. Regional activation results

All the results correspond to second-level analyses including behavioral outcomes as covariates of interest (see details in Section 2.5.3). No significant associations were found between any behavioral variable and neural activation in any condition. Contrasting the reading conditions (L1R vs. L2R) resulted in no significant activations. Conversely, no significant activations were observed in the contrast of FT vs. BT, nor in the comparison between FT and BT relative to their respective baseline reading conditions.

3.3. PPI results

Reading trials with a score of 0 and translation trials with a score below 3 were excluded from analysis. This resulted in the removal of very few trials (L1R = 1%, L2R = 1.5%, BT = 1%, FT = 2%), there being no significant differences between the reading ($\chi^2_{\text{Yates}} = .60$) or the translation ($\chi^2_{\text{Yates}} = .23$) conditions.

Although the ATL may be subject to distortion and signal dropout in fMRI (Devlin et al., 2000), tSNRs for this ROI surpassed the value of 60 for the mean of the whole sample and also for each subject individually (see Supplementary Figure 1), indicating that the signals analyzed were of good quality (Marcus et al., 2013; Murphy et al., 2007). The mean tSNR from all subjects was 89.35 ($SD = 24.16$).

As was the case with regional activation results, all reported results correspond to second-level analyses including behavioral outcomes as covariates of interest (see details in Section 2.5.5). No significant associations were found between any behavioral variable and FC patterns in any condition. Results for the left ATL seed (Table 1) revealed no significant clusters when comparing the reading (L1R vs. L2R) or the translation (FT vs. BT) conditions.

Table 1. PPI results (local maxima) with seed in the left ATL.

Contrast	Region connected with left ATL (L: left; R: right)	Cluster k	x	y	z	Peak t	Peak z
L1R vs. L2R	No suprathreshold clusters were found.						
FT > L1R vs. BT > L2R	L-Superior parietal lobule	122	-15	-64	40	4.90	4.39
	L-Precuneus		-21	-58	43	4.63	4.19
	L-Superior parietal lobule		-30	-64	52	4.48	4.07
	L-Inferior frontal gyrus (pars triangularis)	94	-36	35	-8	4.75	4.28
	L-Orbitofrontal cortex		-33	44	-2	4.39	4.00
	L-Inferior frontal gyrus (pars triangularis)		-39	38	1	4.16	3.83
	L-Precuneus	50	-3	-55	70	5.11	4.54
	L-Precuneus		-15	-52	67	4.95	4.42
	R-Precuneus		6	-52	67	4.37	3.99
BT > L2R vs. FT > L1R	R-Thalamus	30	3	-10	-5	4.84	4.34

Notably, however, significant directionality effects were observed upon direct comparisons of FC differences between FT and BT relative to their respective baseline reading conditions. FT involved three clusters exhibiting FC with the left ATL (Figure 2A). The first was localized in the left IFG, including the pars triangularis and the left orbitofrontal cortex. The other two were located in the bilateral parietal lobes, including the left superior parietal lobule, the left cuneus, and the bilateral precuneus. On the other hand, relative to FT-minus-L1R, BT-minus-L2R was characterized by increased FC between the left ATL and the right thalamus (Figure 2B).

Finally, results for the left IFG and the left pMTG seeds revealed no suprathreshold clusters in any contrast, indicating that connectivity between this hub and other regions was similar across conditions.

Connectivity differences between translation directions

A. FT > L1R minus BT > L2R

B. BT > L2R minus FT > L1R

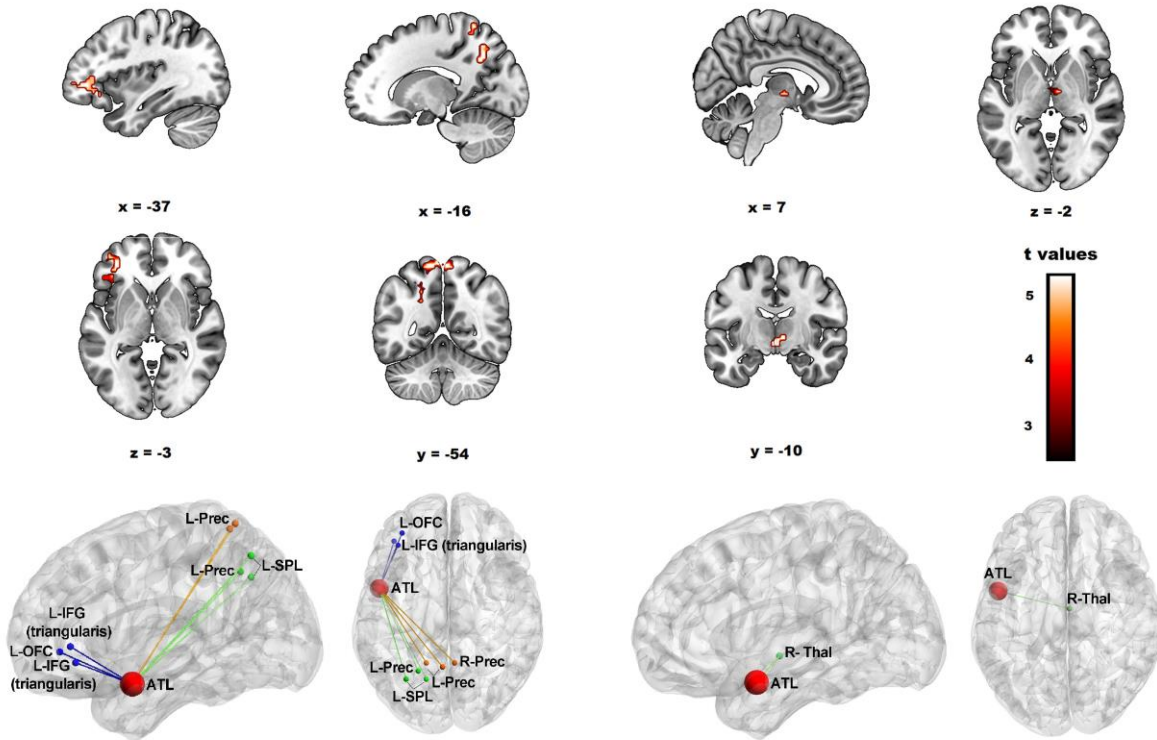


Figure 2. Connectivity differences between translation directions. (A) Comparison between FT and BT, relative to their respective baseline reading conditions showed that the ATL was functionally connected with the left IFG, the orbitofrontal cortex and the parietal lobes, including the left superior parietal lobule, the left cuneus, and the bilateral precuneus. (B) Comparison between BT and FT, relative to their respective baseline reading conditions, revealed increased connectivity between the ATL and the right thalamus. L1R: first-language reading; L2R: second-language reading; BT: backward translation; FT: forward translation. L: left; R: right; ATL: anterior temporal lobe; IFG: inferior frontal gyrus; OFC: orbitofrontal cortex; Prec: precuneus; SPL: superior parietal lobule; Thal: thalamus.

4. Discussion

Our results revealed consistent and selective directionality effects. Mean accuracy was similar for both reading conditions, but significantly worse for FT than BT. Although directionality differences do not always emerge in behavioral measures (Klein et al., 1995; Price et al., 1999), the poorer performance observed for FT mirrors previous results from word- and text-translation tasks (Hatzidaki & Pothos, 2008; Jost et al., 2018), including evidence of more omissions for FT than BT (Darò et al., 1996; de Groot et al., 1994). Broadly speaking, this pattern suggests that FT may imply greater cognitive effort than BT, as postulated in classic (Kroll et al., 2010) and recent (Dijkstra et al., 2018) models of bilingual processing.

More crucially, each direction presented different FC patterns involving the left ATL. This region is critical for multimodal semantic processing, playing putative roles in operations like categorization, semantic priming, and semantic integration (Lambon Ralph et al., 2017; Patterson et al., 2007). Furthermore, the ATL proves crucial for establishing fine-grained semantic distinctions that generalize between-languages (Correia et al., 2014), suggesting a

role of conceptually-mediated processes in the observed FC effects. Of note, the lack of significant differences between BT and FT for another semantically sensitive ROI (namely, the left pMTG) highlights the potentially distinct relevance of ATL connectivity as a signature of the observed directionality patterns.

Specifically, after correcting for potential baseline differences in reading, FT involved greater connectivity of the left ATL with the left IFG, the left orbitofrontal cortex, and the bilateral parietal lobes. In line with our hypothesis, all three hubs are part of the frontoparietal and the vigilance networks, which mediate varied attentional processes, such as the selection of memories, knowledge units, and task-relevant responses (Corbetta, 1998; Shen et al., 2016). In particular, activity along the frontoparietal network indexes processing costs during deliberate language selection (Zhang et al., 2015), with greater engagement for L1-L2 than L2-L1 processes (Wang et al., 2007). Compatibly, evidence from switching tasks suggests that attentional demands, indexed by activity increases in parietal and frontal regions, constitute a core factor underlying asymmetries between L1- and L2-initiated processes (Wang et al., 2009; Wang et al., 2007). Indeed, activation increases for FT relative to BT have also been observed in circumscribed regions subserving attentional (Jost et al., 2018) and semantic (Quaresima et al., 2002; Rinne et al., 2000; Tommola et al., 2001) processes.

It is worth emphasizing that these increased FC patterns for FT were accompanied by poorer behavioral outcomes. While previous studies based on regional activation analyses have also found that FT involves stronger activation than BT in individual language-relevant regions (Klein et al., 1995; Rinne et al., 2000; Tommola et al., 2001), our results indicate that the greater difficulty of FT would reflect increased demands placed on the *integration* of semantic and attentional mechanisms. In other words, we propose that greater FC for the more challenging condition (FT) would entail higher cognitive costs, leading to poorer performance. In line with this interpretation, previous PPI analyses also showed greater FC between the ATL and fronto-posterior hubs as a correlate of increased cognitive effort in tasks requiring explicit attention to meaning (Jackson et al., 2016). Compatibly, then, the particular FC patterns characterizing FT might represent a signature of lower performance due to increased co-activation efforts between semantic and attentional mechanisms.

Instead, upon correcting for baseline reading effects, increased left ATL connectivity for BT was observed only with the right thalamus. Interestingly, thalamic activity has been shown to be greater for L2-L1 than L1-L2 processes during language-switching (Wang et al., 2007). Still, while such results have been proposed to reflect attentional demands (Wang et al., 2007), our findings point in a different direction. First, although the thalamus certainly contributes to attentional processes, its most distinctive functions involve the automatic relaying of sensory information to cortical regions (Fama & Sullivan, 2015; Van Der Werf et al., 2003). Therefore, its greater coupling with the left ATL during BT, alongside the reduced FC patterns involving putative attentional hubs and the better behavioral outcomes observed for this direction, could be better interpreted as less reliance on effortful top-down mechanisms. Moreover, increased connectivity between the thalamus and the ATL may also reflect greater demands for activating L2 (as opposed to L1) input. Indeed, much like the ATL (Lambon Ralph et al., 2017; Patterson et al., 2007), the thalamus has been implicated in lexico-semantic retrieval (Pergola et al., 2013), a process that involves greater electrophysiological modulations for L2-L1 than L1-L2 tasks, including semantic priming (Phillips et al., 2006) and translation (Christoffels et al., 2013). Thus, the FC pattern observed for BT may reflect an increased reliance on bottom-up sensory mechanisms together with greater demands for accessing source-language information.

The relevance of FC metrics to capture differences between both translation directions is reinforced by the results of the regional activation analyses, which failed to discriminate between L1R and L2R and, more crucially, between BT and FT (even when these were

controlled for their respective baseline reading conditions). Such null results reinforce the view that FC approaches can reveal significant differences between BT and FT even when both conditions are not discriminated via univariate approximations –which further attests for the need to include cross-regional integration approaches in the agenda of brain-based translation research (García, 2019) and cognitive neuroscience at large (Mišić & Sporns, 2016).

Interestingly, however, results from the left IFG seed revealed no FC differences between BT and FT. A possible reason behind these null effects concerns the putative role that this region plays in morphosyntactic processing (Ullman, 2001b; Zaccarella & Friederici, 2016). As it happens, sentences in the two languages were carefully matched for multiple variables, including several morphosyntactic features. Therefore, it may be that their parsing and comprehension did not involve differential co-activation patterns between morphosyntactic systems and other relevant cognitive mechanisms –a conjecture that is reinforced by the subjects’ high L2 proficiency but still calls for further research. Tentatively, then, the main differences between FT and BT in high-proficiency bilinguals could lie in the integration of attentional and semantic (as opposed to morphosyntactic) processes. Alternatively, and more speculatively, null results for the IFG seed might partly reflect this region’s involvement in oral production skills (Flinker et al., 2015). In this sense, note that our sample comprised highly proficient bilinguals, whose elevated L2 production skills are probably as high as in L1. In fact, direct comparisons of L1R and L2R yielded neither behavioral nor FC differences, suggesting similar single-language production efficiency for both within-language tasks. Still, this conjecture should be directly explored in other studies directly manipulating oral production demands with and between BT and FT.

More generally, our results foreground the limitations of models that account for bilingual asymmetries by exclusive reference to linguistic systems (Dijkstra et al., 2018; French & Jacquet, 2004). The RHM, for example, explains the directionality effect in terms of how strongly the L1 and L2 word-form systems are connected with each other and with the (shared) conceptual system (Kroll & Stewart, 1994; Kroll et al., 2010). In particular, vocabulary knowledge would be less developed in L2 than in L1 and the links between the word-form systems would be stronger for BT than FT. Moreover, as demonstrated by categorical interference paradigms, only the latter condition would require conceptual mediation, thus calling on longer, slower connections (Kroll & Stewart, 1994; French & Jacquet, 2004; García, 2015).

This framework might well account for the semantic factors of our results. Indeed, FT yielded lower accuracy rates than BT (in line with the postulation of weaker form-level links leading from L1 to L2 and less developed vocabulary in the latter language) and FC differences between both conditions systematically involved the ATL –a critical hub mediating multimodal semantic processes (Lambon Ralph et al., 2017; Patterson et al., 2007). However, the strictly linguistic perspective of the RHM could hardly explain the systematic involvement of key hubs from the frontoparietal and vigilance networks for FT over BT, as their co-activation has been systematically related to attentional processes not only in non-verbal paradigms (Corbetta, 1998; Shen et al., 2016) but also, and more crucially, in cross-linguistic tasks (Wang et al., 2007, 2009; Zhang et al., 2015). Indeed, the absence of cognitive control mechanisms in computational extensions of the RHM has been signaled as a main limitation towards a realistic conception of translation and other verbal processes in bilinguals (Dijkstra et al., 2018a, 2018b). In line with this position, our results suggest that an exclusively linguistic interpretation of the directionality effect may be partial, at best, or unduly simplistic, at worst.

Conversely, our findings support other accounts which propose that such asymmetries are driven by both linguistic *and* domain-general operations (Dijkstra & van Heuven, 2002;

Green, 1998). For example, the inhibitory control model (Green, 1998) posits that linguistic processing in bilinguals is mediated by a supervisory attentional system that regulates its engagement depending on task demands. Such a system is crucial during verbal processing in this population: given that even single-language (e.g., L2) operations entail activation of the subjects' other language (e.g., L1) (Oppenheim et al., 2018; Rodriguez-Fornells et al., 2006; Thierry & Wu, 2007), supervisory attentional mechanisms must be recruited to select an adequate language schema at each processing step and prevent the non-selected language from reaching supra-threshold activation levels (Green & Abutalebi, 2013). Nevertheless, due to the differential entrenchment of the L1 and the L2 in bilingual memory, these control demands are greater when the subject must switch from the more dominant to the less dominant language (typically, the L1 and the L2, respectively) than when the task involves the opposite language sequence (Costa & Santesteban, 2004).

Therefore, compared to BT, FT would involve a larger attentional effort to inhibit the dominant language (L1) during source-text processing and activate adequate words in the weaker language (L2) during target-text production. In other words, each direction would implicitly tax supervisory attentional mechanisms to a different degree, as cross-linguistic regulation is differentially engaged when recurring from L1 or L2 inhibition. Together with previous studies (Christoffels et al., 2013; García et al., 2016; Jost et al., 2018), our research offers neurobiological support for this perspective, suggesting that directionality effects reflect the coupling of both linguistic *and* cognitive control operations.

5. Limitations and avenues for further research

Despite their potential importance, the conclusions above must be considered as preliminary and assessed against some main limitations. First, our sample size was moderate. Although most previous neuroscientific studies on directionality have actually yielded replicable results with considerably smaller groups (e.g., Christoffels et al., 2013; Jost et al., 2018; Klein et al., 1995; Price et al., 1999), future experiments should aim for larger *Ns*. Second, experimental materials were confined to 24 items per condition. This enabled us to select only those sentences that were effectively matched across multiple variables, but it would be desirable to replicate our study with more extended stimulus sets.

Third, the use of unaltered naturalistic materials from an English corpus meant that sentences varied in register. While this contributed to the ecological validity of our stimuli, such a stylistic feature was not systematically manipulated in the present design, opening an unexplored avenue for future investigation. Besides, as in other neuroscientific studies on translation (Christoffels et al., 2013; Hervais-Adelman et al., 2015a; Hervais-Adelman et al., 2015b; Jost et al., 2018; Klein et al., 1995; Price et al., 1999; Rinne et al., 2000), the use of overt production allowed us to assess the accuracy of the participants' responses but it may have introduced motor artifacts. Even though articulatory confounds were likely cancelled out across conditions, it would be useful to examine whether similar results are obtained in silent translation tasks. Fourth, at the time of testing, our setup did not allow for tracking response times. Although previous evidence of similar response latencies for BT and FT in high-proficiency bilinguals (García, 2015; Garcia et al., 2014; Santilli et al., 2018; van Hell & de Groot, 2008) suggests that this factor likely played no major role in the observed results, it would be important for future replications of our work to complement assessments of accuracy with response time measures.

Additional reservations should be acknowledged regarding the use of double contrasts (FT-minus-L1R vs. BT-minus-L2R). Granted, this is an established approach in neurocognitive translation research (Price et al., 1999; Rinne et al., 2000; Tammola et al.,

2001) and its employment allowed us to maximize comparability between present results and key previous findings while partly ruling out potential source-language-related confounds. However, this approach also carries potential interpretive limitations, especially because the observed differences may be driven by either interlingual reformulation proper or by articulatory discrepancies between L1 and L2 production. In this sense, future neurocognitive research on directionality should contemplate novel control tasks capable of teasing apart the modulations underlying each of those sub-stages during the translation process (García, 2019).

In addition, note that our FC analyses were based on a lenient threshold with an uncorrected $p < .001$ and a minimal cluster size of $k = 30$. Although the same threshold has been employed in previous studies using PPI analyses (Baeuchl et al., 2015; Li et al., 2018; Osumi et al., 2012; Steuwe et al., 2015) to balance the risk of type I and type II errors (Lieberman & Cunningham, 2009), future studies should examine other potential FC differences between BT and FT using metrics that allow for more strict thresholding methods. Finally, it must be noted that our results may have been influenced by the size established for our ROIs (which had radiuses of 10 mm). Although previous FC studies on language (Callan et al., 2005; Jackson et al., 2016; Takashima et al., 2017) as well as PPI studies targeting other neurocognitive domains (Eger et al., 2007; Genon et al., 2013; Wagner et al., 2013) have considered ROIs of similar size, and despite the relevance of employing relatively wide ROIs when targeting anatomically broad regions, future studies should test whether similar results are obtained when manipulating the size of ROIs, ideally aiming for greater neuroanatomical precision.

6. Conclusion

In sum, this is the first fMRI study assessing FC differences between FT and BT. Our results suggest that FT involves enhanced coupling between semantic and attentional mechanisms, as a correlate of poorer behavioral performance. This finding supports the view that asymmetries in bilingual processing are driven by functional interactions between linguistic and domain-general systems. Future research along these lines may further illuminate the complex neurocognitive interplays underlying cross-linguistic processing in bilinguals.

Conflict of interest

The authors declare no association that poses or could be perceived as a financial or intellectual conflict of interest in connection with the manuscript.

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